OBSERVATIONS ON TUPAIA, WITH REFLECTIONS ON THE ORIGIN OF PRIMATES.

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According to many anatomists, "the *Tupaiæ* possess a large cœcum."[1] It appears worthy of mention, therefore, that on opening recently the abdominal cavity of a specimen of *Tupaia ferruginea* from Borneo not a trace of a cœcum was to be seen (Pl. IX, fig. 1), confirming the statement recently made by the writer[2] that the cœcum was not invariably present in that Insectivore, nor was it present in a recently examined specimen of *T. pictum*. It may be stated, in a general way at least, that in mammals in which the stomach is large the cœcum is small, and *vice versa*. This inverse relation of the stomach and cœcum as regards size appears to be conditioned by the fact that in cases where gastric action is limited by the small size of the stomach, the lack of digestion is made up by the digestive action that goes on in the cœcum. It is not to be supposed, however, that the cœcum secretes a digestive juice like that of the stomach, but rather that the proteid elements of the food and the acids developed from the latter by fermentation act upon the residue of the food in the cœcum like the pepsin and hydrochloric acids of the gastric juice.

In cases, therefore, in which the stomach is large, as in that of the *Tupaia* examined, it might be expected that the cœcum would be found to be small, or even altogether absent. As a matter of fact, in the specimen of *Tupaia* dissected the stomach was relatively large, measuring in its long diameter 5 cent. (2 inches), the animal itself, from the vertex to the root of the tail, measuring only 20 cent. (8 inches).

The stomach was found distended to its utmost capacity, presenting an almost globular form, and filled with what appeared to be principally the remains of vegetable food, though some remains of insects were present. As gastric digestion appeared to be largely accomplished by the stomach in the case of the *Tupaia* examined, the entire absence of a cœcum becomes, after what has just been said, intelligible. The intestine, measuring 71.2 cent. (28.5 inches), exhibited throughout a uniform diameter, and was loosely suspended from the duodenum to the rectum by a continuous fold of peritoneum.

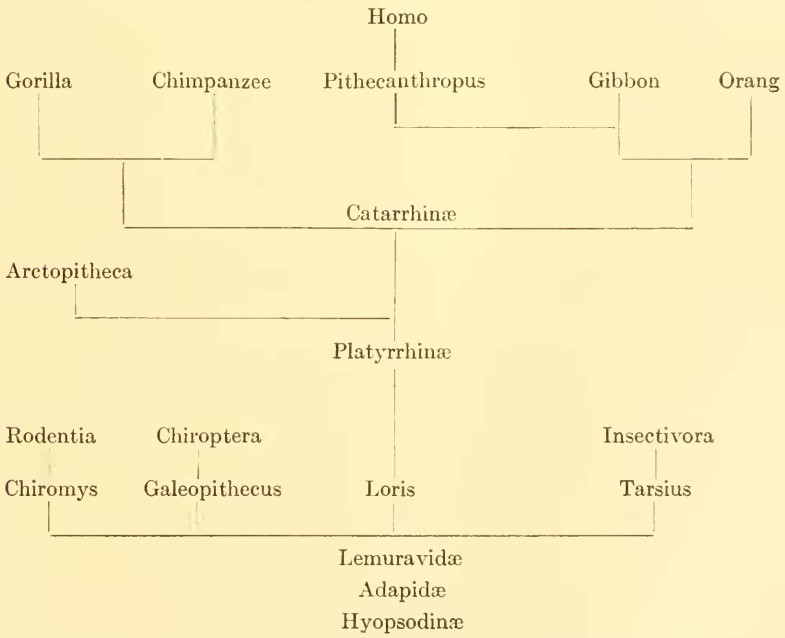
[1] Huxley, *Anat. of Vertebrated Animals*, 1872, p. 383; Carus, *Zoologie*, 1868–75, S. 89.

[2] *Proc. Acad. Nat. Sci. Phila.*, 1902, p. 249.

The liver was divided into four lobes, the gall bladder lying as if in a hole in the cystic fissure.[3] The common bile duct passed into the intestine .5 cent. (one-fifth of an inch) from the pylorus, that of the pancreas about an equal distance from the orifice of the bile duct.

As *Tupaia* is usually regarded as being in its affinities the most lemurine of the Insectivora, and *Tarsius* the most insectivorous of the lemurs, the alimentary canal of *Tarsius spectrum* recently dissected by the author (Pl. IX, fig. 2) is submitted for comparison with that of *Tupaia*. It will be observed that in *Tarsius* a distinct cœcum is present, though not large, and that the stomach is very small.

In previous communications made to the Academy, the author called attention to the affinities of *Chiromys* and the Rodentia,[4] *Galeopithecus* and the Chiroptera.[5] If the structure of these animals has been correctly interpreted, and it be further admitted that *Tarsius* stands in a similar relation to the Insectivora, and *Loris* (*Stenops*) to the Simiæ, the phylum of these various orders would be related to each other somewhat as follows:



[3] Hunter, *Essays and Observations on Nat. History*, edited by Owen.
[4] *Proc. of Acad. Nat. Sci. Phila.*, 1900.
[5] *Proc. Acad. Nat. Sci. Phila.*, 1902

If speculation be further indulged in as regards the manner in which the descendants of cretaceous or eocene lemurs could be transformed into Platyrrhine monkeys like those living at the present day, it is readily seen, as suggested by Leidy,[6] "that but little change would be necessary to evolve from the jaw and teeth of *Notharctus* that of a modern monkey. The same condition which would lead to the suppression of a first premolar in continuance would reduce the fangs of the other premolars to a single one. This change with a concomitant shortening and increase of depth of the jaw, would give the character of a living *Cebus*. A further reduction of a single premolar would give rise to the condition of the jaw in the Old World apes and man." In the union of the rami of the jaw at the symphysis, in the small size of the condyle, in the number of the incisors, canines and true molars, nearly alike in their constitution and in their crowded condition, the lower jaw of *Notharctus* resembles most strikingly that of a Platyrrhine monkey. Like Leidy, both Cope and Marsh regarded the Platyrrhine monkeys, on the one hand as the descendants of extinct lemurs, and, on the other, as the ancestors of the Catarrhinæ.

Thus Cope,[7] basing his view upon the structure of *Tomitherium*, offered as a possible phylum the following:

Homo
|
Simiidæ
|
Cebus
|
Hapale
|
Lemur
|
Tomitherium

though later, as we shall see presently, he modified the above view[8] somewhat, finally regarding man and the anthropoids as having probably descended directly from extinct lemurs like *Anaptomorphus*. By similar reasoning from the study of closely affiliated, if not identical, Lemuroid genera: *Limnotherium* (*Tomitherium*), *Antiacodon* (*Anaptomorphus*), Marsh,[9] in referring to the origin of the Primates, was led to the conclusion that "we may justly claim America for the birthplace of the order."

Why the Old World apes, when differentiated, did not come to the

[6] *Extinct Vertebrate Fauna*, 1873, p. 90.
[7] Mammalia Educabilia, *Am. Phil. Soc.*, 1873.
[8] Lemuroidea, etc., *American Naturalist*, 1885, p. 467.
[9] *Vertebrate Life in America*, 1877, p. 52.

land of their earlier ancestry is readily explained by the then intervening oceans, which likewise were a barrier to the return of the horse and rhinoceros. Man, however, came doubtless first across Behring's Straits, and at his advent became part of our fauna as a mammal and primate.

As a confirmation of the view that the Platyrrhinæ have descended from monkeys, it may be mentioned that while the remains of *Cebus*, *Myctes*, *Callethrix*, and *Hapale* have been found, according to Ameghino,[10] in the Pleistocene strata of Brazil, extinct lemurs, such as Notopithecidæ and Homunculidæ, have been discovered recently, according to the same high authority, in the eocene deposits of South America.[11] Indeed, according to Ameghino,[12] the Homunculidæ are to be regarded as the "ancêtres de tous les singes du nouveau que de l'ancien continent les lémurs excepte." Cope appears to have taken the same view as that expressed by Ameghino. In speaking of certain extinct forms of monkeys found in Patagonia, he remarks that they "appear to be ancestors of the existing South American monkeys (Cebidæ), and possibly of the Old World monkeys also."[13]

It should be mentioned, however, that these fossils are regarded by some paleontologists as being rather the remains of Platyrrhine monkeys than lemurs. Should such prove hereafter to be the case, it will not weaken the argument, since in that case the forms in question, if not lemurs, would be intermediate in character between the latter and Platyrrhine monkeys. The remains of Catarrhine monkeys, such as *Papeo*, *Macacus*, *Semnopithecus*, and possibly even of the chimpanzee and orang, have been found in the Pliocene deposits of India.[14]

Such facts are, however, not inconsistent—indeed, have little or no bearing upon the question of the derivation of Catarrhine from Platyrrhine monkeys—since the only assumption that would be necessary would be to suppose that the Platyrrhine ancestors of the fossil Pliocene Catarrhines existed once in India or elsewhere. It may be said, however, that this is assuming the very question at issue, a case of *petitio principii;* but the reverse proposition, that the Platyrrhine have descended from the Catarrhine monkeys, is untenable, being inconsistent with the well-established fact that the more ancient members of a group of animals had always more teeth than the later more recent

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[10] *Actas Sciencias Cordoba*, T. VI, 1889, p. 101.
[11] *Bol. Acad. Nac. Buenos Aires*, T. XVII, 1902, p. 7.
[12] *Op. cit.*, T. XIII, 1902, p. 265.
[13] *Organic Evolution*, 1896, p. 154.
[14] Flower and Lyddeker, *Mammals Living and Extinct*, 1891, pp. 723, 727, 738.

members of the same. Thus among the Prosimiæ, for example, the oldest members of the group, the Hyopsodinæ, possessed 44 teeth = $\frac{3.1.4.3}{3.1.4.3}$ in each jaw, the more recent Adapidæ 40 teeth = $\frac{2.1.4.3}{2.1.4.3}$, the most recent Lemuridæ 36 teeth = $\frac{2.1.3.3}{2.1.3.3}$, the Platyrrhinæ 36 teeth with the exception of the *Arctopithecа* 32 teeth = $\frac{2.1.3.2}{2.1.3.2}$, and finally the Catarrhinæ, including the anthropoid apes and man, 32 teeth = $\frac{2.1.2.3}{2.1.2.3}$. It is highly improbable, if not impossible, therefore, to say the least, that Platyrrhine monkeys with 36 teeth should have descended from Catarrhine ones provided with only 32; that 4 premolar teeth, absent in the ancestors, once lost, should reappear again in their descendants—an objection that equally applies to Cope's derivation of *Cebus* with 36 teeth from *Hapale* with 32, as previously mentioned.

Further, the Platyrrhine monkeys resemble lemurs in many more respects than in the mere number of the teeth, thus showing their inferior position in zoological rank as compared with the Catarrhines. Thus, for example, the oblique ridge extending from the anterior internal cusp (protocone) to the posterior external cusp (metacone) of the upper molars in *Ateles* and *Myctes*, and many other South American monkeys, is present in certain lemurs, such as *Nycticebus, Arctocebus, Loris,* as also in anthropoid apes and man, though absent in the remaining Catarrhines.[15] Now the presence of this oblique ridge in the upper molars of lemurs, apes and man was regarded by so high an authority as Cope as such an important feature in their structure that it largely influenced that great paleontologist in suggesting the view, already alluded to, that man and apes are the direct descendants of lemurs rather than of Catarrhines.

It is obvious, however, that if Cope's argument is of any force in the above instance, it must be of even greater cogency in showing that Platyrrhine monkeys have descended from lemurs, since lemurs and Platyrrhinæ not only exhibit the "oblique ridge" in their molars, but possess many other structural features in common, whereas lemurs are relatively so low in the zoological scale that they are not regarded by most anatomists as being primates at all. Indeed, Cope might just as well have argued that man has descended from a Platyrrhine monkey as from a lemur, the evidence adduced being about as good for the one view as the other; for even if the "centre of motion" of the vertebral column and the "anticlinal vertebra," the number of vertebræ entering into the formation of the sacrum, etc., are only the same in man, anthropoids and *Nycticebidæ*,[16] nevertheless in other respects—in fact,

[15] Tomes, *Dental Anatomy*, 1876, pp. 7, 370.
[16] Flower, *Osteology of Mammalia*, 1870, pp. 47, 24, 60.

in the totality of their organization—man and anthropoids resemble the Catarrhine monkeys far more than lemurs. Had Cope, at the time he described *Anaptomorphus*, been aware that the placenta of *Tarsius*, a closely affiliated lemur, was discoid in form and highly complex in structure rather than diffuse and non-deciduous, as in other lemurs, his view of the lemuroid descent of man would have been strengthened by an argument of far more weight than one based upon the presence of an oblique ridge on certain teeth and the number of sacral vertebræ, which vary even in different individuals of the same or closely allied species. Apart from the number of the teeth being the same in Platyrrhines and lemurs, the lemuroid character of dentition of the former is clearly manifested by the long narrow inferior incisors of the South American Saki (*Pithecea*).

Further, in all Platyrrhine monkeys, as in most lemurs, the base of the petrosal bone is excavated by that part of the lateral cerebral venous sinus terminating at the postglenoid fossa. Similarly in both lemurs and Platyrrhines the malar bone is perforated by that branch of the facial nerve known to the classical anatomist as the "nervus subcutaneus malæ." Again, in many Platyrrhines—as, for example, in *Cebus, Ateles, Nyctipithecus*—a small unossified vacuity is exhibited in the bony plate separating the orbital from the temporal fossa, evidently the relic of the space by which the two fossa freely communicate in the lemurs.

In all the South American monkeys the tympanic bone retains more or less its primitive ring-like form, the cavity of the tympanum lying close to the external wall of the cranium, its inferior surface, together with that of the anchylosed penotic bone, exhibiting a very swollen appearance. In this respect the Platyrrhine monkeys agree with the lemurs, in which the inferior surface of the tympanum presents a large rounded bulla, and differ from all Old World monkeys, in none of which an auditory bulla is ever present. The otosteals of the Platyrrhines resemble those of lemurs more than those of Catarrhines, monkeys, apes or man.

It is an interesting fact, also, that while the macula lutea is present in the eye of man, apes and Catarrhines, it has never been found, so far as known to the writer, in any Platyrrhine or lemur.

As reference has been made to the character of the vertebræ in man and Nycticebidæ, it may be as well mentioned in this connection that in the lemur *Galago* the posterior edges of the spinous processes of the lumbar vertebræ present a pair of processes which, projecting backward, clasp the anterior edges of the succeeding spinous process, and

that similar processes, though not so well developed as in *Galago*, are present in certain species of South American monkeys, as, for example, in *Lagothrix* and *Myctes*. The presence of these processes is quite as strong a proof that Platyrrhines have descended from lemurs as are the peculiarities in the vertebral column already referred to that man has descended directly from a lemur. It is well known that while the supracondylar perforation of the humerus is not found in any Old World monkey, nor in *Hapale*, *Ateles* or *Myctes* among those of the New World, nevertheless such perforation is found in the Cebidæ and most of the lemurs. It would be tedious to show in further detail that, as regards the muscular system, the character of the brain, the larynx, the alimentary canal, and in many other respects, the Platyrrhine monkeys are less specialized than the Catarrhines, which has induced the majority of anatomists to regard the New World monkeys as of higher rank zoologically than the lemurs, but lower in the scale of life than the Catarrhines, occupying an intermediate position between the two. This is consistent with the view that they are the descendants of the one and the ancestors of the other.

This conclusion has been confirmed in late years by the remarkable researches of Selenka,[17] Strahl,[18] and others, who have shown, in a general way at least, that the transitory stages through which the placenta of man and anthropoids pass are permanently retained as the placenta of certain marsupials, lemurs, *Tarsius*, Platyrrhines, Catarrhines, illustrating the law that in the development of the placenta the ontogeny is as elsewhere the epitome of the phylogeny.

Thus while in marsupials like *Macropus* the allantois remains free, as first shown by Owen,[19] and nearly fifty years afterward by the writer,[20] in *Perameles* and *Dasyurus* the allantois, it is said, adheres to the mucous wall of the uterus, forming at least the beginning of a placenta, without, however, a decidua or chorionic villous process being developed. In lemurs, while no decidua is as yet developed, the chorion exhibits villous processes which insinuate themselves into the mucous wall of the uterus. In *Tarsius*, however, the allantois begins to form a true disk-like placenta with a veritable decidua—"nicht eine lockere gross zottige diffuse Placentation wie Lemur und Nycticebus sondern eine hoch komplicirte und diskoide Placenta besitzt."[21]

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[17] Selenka, *Studien über Entwickelungsgeschichte der Tiere*, 1900, S. 176.

[18] Strahl, in O. Hertwig's *Entwickelungslehre der Wirbeltiere*, Dritte Lieferung, 1900, S. 235.

[19] *Phil. Trans.*, 1834, 27.

[20] *Proc. Acad. Nat. Sci. Phila.*, 1881.

[21] Hubrecht, *Die Keimblase von Tarsius*, 1896, S. 15.

The placenta of the New World monkeys exhibit a step further in advance the difference from the placenta of *Tarsius*, being however, one of degree rather than of kind.

In the Old World monkeys the allantois forms a double placenta, a primary large dorsal one and a secondary small ventral one (Plate X). While this appears to be normally the case, it should be mentioned that the writer observed but one placenta in the case of a pregnant female of *Macacus cynomolgus* examined by him, though the pregnancy was far advanced in both instances.[22] It will be observed that in the case of the *Macacus* (Plate X), the two placentas are not entirely separated as is usually the case in Catarrhines, being joined by a small body of tissue.

It is also a significant fact that while two umbilical veins and two umbilical arteries are always present in the umbilical cord of the New World monkeys, but one umbilical vein is present in that of the Old World ones. Finally, the placenta of the anthropoids agrees essentially with that of man.

In the opinion of the writer, therefore, the phylum submitted at p. 149, essentially that of Haeckel,[23] expresses about the truth as to the descent of man, etc., so far as can be learned at present from the facts of palæontology, comparative anatomy and embryology, that bear upon the question. That the ancient Prosimiæ, Hyopsodinæ, Adapidæ, etc., have descended from some ungulate type of life is manifested by their affinities with the latter group of mammals. Indeed, Cuvier described *Adapis* as "un autre genre de pachyderme —et que je nommerai provisoirement Adapis,"[24] while, according to Leidy, *Notharctus tenebrosus* was "a small extinct pachyderm, resembling that of some of the existing American monkeys quite as much as it does that of any of the living pachyderms."[25]

It is quite possible that future researches may show that there is no genetic connection between *Chiromys* and the Rodentia, but that the rodent-like teeth of the former and of the wombat may have been acquired independently by a process of natural selection, it being easy to see, according to Tomes,[26] "how a rodent type of dentition is beneficial to its possessor by rendering accessible articles of food wholly unavailable for creatures which have no means of gnawing through a

[22] *Proc. Acad. Nat. Sci. Phila.*, 1879, p. 146.
[23] *Anthropogenie*, Zweiter Band, 1903, S. 650.
[24] *Ossemens Fossiles*, Tome 5me, 1835, p. 460.
[25] LEIDY, *op. cit.*, pp. 86, 89.
[26] *Op. cit.*, p. 249.

shell or other hard body," the theory being, according to Darwin, that a small variation arising in the dentition through some nutritive change, and being of advantage in the struggle for life, would be intensified in successive generations until, in the end, a type of tooth would be evolved such as is presented in the case of the wombat, *Chiromys*, and Rodentia living in far distant parts of the world.

Finally, in the judgment of the writer, man cannot have descended from either the gorilla, chimpanzee, the orang or gibbon, since, apart from the structural difference between any one of them and man being too great to warrant such an hypothesis, the three great anthropoid apes are obviously degenerates leading to no higher form of life, but rapidly dying out, as shown by the fact that these apes resemble man much more when very young than when adult. While it is true that the gap between man and the gibbon is greater than between man and the remaining apes, nevertheless, as *Pithecanthropus erectus*, whatever its real nature may be, is something more than a gibbon, and yet something less than a man—more ape-like than any man, and more man-like than any ape[27]—by a method of exclusion the conclusion is reached that the man and gibbon are related in some way.

It must be admitted, nevertheless, that the question of the exact origin of man is largely as yet one of speculation, and that future researches may show that our ancestors may have been extinct Catarrhine or Platyrrhine monkeys or even lemurs.

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[27] E. Dubois, *Pithecanthropus Erectus*, 1894.
O. C. Marsh, *On the Pithecanthropus*, etc., 1895.
Schwalbe, Studien über Pithecanthropus erectus, *Zeits. für Morph. v. Anthr.*, 1899, S. 16.